17. The Classification of the Sciuridæ. By R. I. Рососк, F.R.S.

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(Text-figures 18-29.)

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Introduction.

In the following brief review * of the more important attempts to classify the Sciuridæ, it is unnecessary to do more than quote Gray's papers, published in 1867 (Ann. Mag. Nat. Hist. (3) xx. pp. 270-286, 323-334, 415-436). The results he achieved were of no great moment from my present point of view, but he introduced a number of new sectional names which have to be borne in mind. In 1880, Trouessart (Le Naturaliste, i. pp. 290-293, 315) made a similar but more successful and useful effort, proposing several new names but ignoring those of Gray as connoting groups composed of unrelated elements. He divided Sciurus into seventeen subgenera, amongst which appear such well-defined forms as Rheithrosciurus and Xerus, which he regarded as equivalent to Neosciurus, Parasciurus, Echinosciurus, and Tamiasciurus, dismembered from Sciurus on certain comparatively trivial characters presented by some of the American species.

The most important contribution to the subject was made in 1893 by Forsyth Major (Proc. Zool. Soc. 1893, pp. 186–190) from a study of the teeth and skulls. He recognised the three subfamilies Sciurinæ, Pteromyinæ, and Nannosciurinæ. The Sciurinæ

^{*} I have not here taken into account the numerous papers on American Sciuridae which belong to four well-marked and universally admitted types—namely Sciurus, Tamias, Citellus, Cynomys, and Marmota. As compared with the true arboreal Squirrels of the Old World, the American species of Sciurus are singularly uniform in essential characters, although a large number of subgenera are admitted. Citellus has been similarly broken up into subgenera, and Eutamias has been dismembered from Tamias.

he divided into six genera:—(1) Rheithrosciurus; (2) Xerus; (3) Sciurus; (4) Citellus (Spermophilus)*; (5) Marmota (Arctomys); (6) Cynomys. Of these, Rheithrosciurus, Citellus, Marmota, and Cynomys were not subdivided; but both Xerus and Sciurus

contained several subgenera.

Xerus was divided into five:—(1) Protoxerus for stungeri, aubinnii and other African species; (2) Xerus for rutilus, capensis, and erythropus; (3) Atlantoxerus for getulus; (4) Paraxerus for cepapi, congicus, isabella, lemniscatus, and other African Squirrels; (5) Funambulus (Eoxerus) for palmarum, tristriatus, and other related Oriental Squirrels. To systematists the interesting point to notice in connection with Forsyth Major's conception of the genus Xerus is the inclusion in it of certain soft-furred arboreal species of African Squirrels (Protoxerus and Funisciurus) and of the Oriental Palm Squirrels (Funambulus), which were previously regarded as more nearly related to Sciurus.

Sciurus, according to Forsyth Major, comprised three subgenera:—(1) Ratufa (Eosciurus) for the large Oriental Squirrels indica, bicolor, etc.; (2) Sciurus, sensu stricto; (3) Tamias for the Chipmunks or Chipping Squirrels. Ratufa and Tamias were undivided; but the species of Sciurus were classified in four unnamed groups: (a) comprising certain African species, annulatus, punctatus, rufobrachiatus, and others; (β) Oriental species, prevosti, caniceps, notatus, ferrugineus, etc.; (γ) vulgaris, syriacus; (δ) carolinensis, astuans, aberti, and other American species.

In 1897 (Proc. Zool. Soc. 1897, p. 933) Thomas revised Major's classification in nomenclature and other points—so far as the genera Rheithrosciurus, Xerus, and Sciurus were concerned. Granting generic value to all Major's subgenera, with the exception of Atlantoxerus which remained a subgenus of Xerus, he assigned the Squirrels to the following eight genera:-Rheithrosciurus, Protoxerus, Xerus, Funisciurus, Funambulus, Ratufa, Sziurus, and Tamias. Under each of these generic names, apart from Rheithrosciurus and Protoxerus, one or more subordinate names appear; but it is not in all instances clear whether these were cited as connoting subgenera or merely as synonyms. In the case of Xerus it seems certain that Geosciurus and Atlantoxerus stood for subgenera; and probably that value was assigned to some at all events of the named divisions of Sciurus, such as Callosciurus and Tamiasciurus. But it is not likely that Rukaria and Eosciurus were looked upon as subgenera of Ratufu; and it is certain that Palmista was quoted merely as a synonym of Funambulus. Nevertheless great service was done by nailing each name so quoted to a type-species.

In 1898, De Winton (Ann. Mag. Nat. Hist. (7) ii. pp. 12-13) attempted to show that Forsyth Major's genus *Protoxerus* was heterogeneous, some of the species being *Xerus*-like and belonging

^{*} In the case of nos, 4 and 5, I have adopted the names now in use for the genera, those employed by Forsyth Major being put in brackets.

to Funisciurus (= Paraxerus Major) and others to Major's section a of the genus Sciurus, for which Trouessart's name Heliosciurus was available. The interest of this paper lies in the circumstance that two authors working on the same material and using the same characters, namely skulls and teeth, came to very different conclusions. De Winton also commented on the curiosity and inconvenience of the fact that in the African Squirrels that approach Xerus in harshness of fur the skull and teeth are Sciurus-like, whereas those with softer fur approach Xerus in cranial characters.

In a paper upon the African Squirrels (Ann. Mag. Nat. Hist. (8) iii. pp. 467-475, 1909) Thomas revised de Winton's and Major's conclusions with respect to the Ethiopian species. As the result of a more exhaustive examination, he came to the conclusion, mainly on the evidence of skulls and teeth, that no fewer than twelve genera should be admitted:—Sciurus for poensis and two others; Heliosciurus for gambianus, punctatus, rufobrachiatus, etc.; Myrsilus for aubinnii and one other; Funisciurus for isabella, leucostigma, lemniscatus, etc.; Paraxerus for cepapi, palliatus, pauli, etc.; Protoxerus for stangeri alone; Epixerus for ebii and wilsoni; Atlantoxerus for getulus; Xerus for brachyotus and rutilus; Geosciurus for capensis; Euxerus for erythropus and microdon; Myosciurus for minutus.

With the exception of *Myosciurus*, retained in the subfamily Nannosciurine, all the rest were referred to the Sciurine. But the genera of Sciurine were divided into two sections, A and B, B containing the four genera *Atlantoscrus*, *Xerus*, *Geosciurus*, and *Euxerus*, distinguishable from the rest of the Sciurine by

their coarse fur and cranial characters.

In connection with these attempts to arrive at the truth with regard to the affinities of the species of Squirrels, it may be noted that both Forsyth Major and Thomas retained a certain number of typical African and Asiatic forms in the genus Sciurus, of which S. vulgaris in the type. This affiliation resulted from the evidence supplied by skulls and teeth; but the conclusion very forcibly suggested by the literature of the subject is the untrustworthiness of such characters.

This conclusion as applied to typical Squirrels was confirmed by Thomas in 1915 (Ann. Mag. Nat. Hist. (8) xv. pp. 383-387) from a study of the penis bone or baculum. To the details of this paper I shall refer in the following pages; but attention may here be drawn to one or two important points that were clearly brought to light:—(1) None of the tropical African* or Asiatic species, except Rheithrosciurus, shows any near affinity to Sciurus. (2) All the American Squirrels ranging from Cauada

^{*} To the African species assigned to Sciurus in 1909, Thomas subsequently gave the name Æthosciurus, with poensis as the type (Ann. Mag. Nat. Hist. (8) xvii. p. 271, 1916), and in 1918 (Ann. Mag. Nat. Hist. (9) i. p. 33) he dismembered the black-striped species of Paraxerus from that genus, calling them Tamiseus.

to South Brazil are closely related to *Sciurus*. (3) The subfamily Nannosciurine must be abolished as composed of heterogeneous

elements, alike only in convergent characters *.

In 1923 (Proc. Zool. Soc. 1922, pp. 1171–1212) I published a paper on the external characters of all the species of Sciuridæ available to me as fresh or spirit-preserved specimens. But for want of adequate material I was compelled to omit consideration of the penis and baculum. To Mr. Thomas's kindness in lending me the collection of bacula prepared under his orders at the Natural History Museum, I now owe the opportunity to figure and describe, not only the specimens of this bone described in general terms in his paper, but also those of a few Petauristidæ, of Citellus, Xerus, and some others which he intended, granted time, to work out himself. To the account of these bacula I have added descriptions of the penis and bacula of such specimens of Sciuridæ as I had preserved for the Zoological Society's collection.

DESCRIPTION OF THE PENIS AND BACULUM.

1. The Palearctic and American Species.

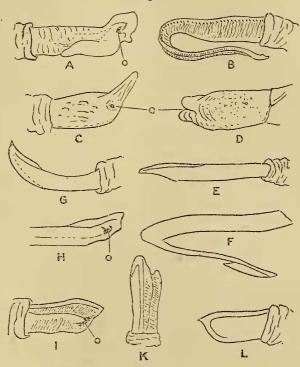
In Sciurus vulgaris the apex of the penis is compressed and upturned where the terminal blade of the baculum runs into it. The orifice opens on the right side behind and below the tip, and is surmounted by a small fleshy lappet; and the small process of the blade of the baculum forms a marginal projection just below and in front of the orifice. The soft swollen tissue enveloping the apex of the penis is continued backwards as a curved crest from above the orifice to terminate near the middle of the dorsal surface of the glans; and laterally and inferiorly it is defined by a groove from the wrinkled, more slender, and rod-like proximal portion of the glans. My observations on this species agree with those of Tullberg, who figured the penis and the extracted baculum from two points of view. (Text-figs. 18, A; 19, A, B.)

I find, moreover, that the glans penis of Sciurus (Neosciurus) carolinensis is of precisely similar structure. Thomas also described the baculum of S. vulgaris, and pointed out that the type of baculum found in that species occurs also in a number of other forms from Asia and North and South America. In the collection of the British Museum the bacula of the following species demonstrate this truth:—S. vulgaris from Europe, persicus from Asia Minor, lis from Japan, niger from North America, carolinensis from Tennessee and England (imported), nayoritensis from Jalisco in Mexico, langsdorffi from the Sierra de Chapada, ingrami from Rio Janeiro, and variabilis from South America. And there is no reason to doubt that the glans penis in all these species conforms to the shape of the baculum. In view of these

^{*} True at all events of the African Myosciurus and the Oriental Nannosciurus, which respectively fall into line with other species of the regions they inhabit. But the baculum of the South American genus has yet to be examined.

facts, Tullberg's statement that the North American species *Tamiasciurus hudsonicus*, always regarded as closely akin to the other Squirrels of that country and as ranking merely as a subgenus of *Sciurus*, has an elongated apically attenuated glans penis

Text-figure 18.



- A. Glans penis of Sciurus vulgaris.
- B. The same of Tamiasciurus hudsonicus.
- C. The same of Funambulus palmarum.
- D. The same of Tamiodes tristriatus.
- E. The same of Callosciurus prevosti.
- F. Penis of the same, with baculum attached, showing position of blade.
- G. Glans penis of Callosciurus notatus.
- H. Apex of same from right side, showing orifice.
- I, K, L .The same of *Tomeutes vittatus* from right side, above, and left side, o. Orifice.

without a baculum, appeared to me to be so remarkable and contrary to all expectations that I wrote to Mr. Gerrit S. Miller, of the Smithsonian Institution, Washington, to ask if he would be good enough to verify the statement for me. In reply, he very

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kindly arranged for two male examples of the species, preserved in alcohol, to be sent to me *. From these two specimens I find that Tullberg was perfectly correct, and had not, as I supposed, made an error of identification. The glans penis in the Alaska specimen is slender and tolerably evenly tapering, with the orifice terminal and just beneath the apex. The upper surface has a median groove, and a pair of crests of minute serrulations running along it, and the sides are finely striolate. The distal portion below the bend is somewhat flattened, and provided on each side with a narrow laminate expansion. In the New York specimen, assigned to the subspecies loquax, the general form and sculpturing of the penis are much the same, except that the striolæ are coarser, the intervening spaces forming fine ridges. a difference possibly due to greater contraction of the epithelium, and the distal portion beyond the bend is not so evenly tapering, but shows an excrescence on each side. Nevertheless the two are of essentially the same type, and in both the distal portion is soft and flexible without a vestige of baculum that I can detect. The structure of the penis sharply differentiates hudsonicus from the Squirrels with the vulgaris type of penis and baculum, and compels the admission of Tamiasciurus as a well-defined genus without any near allies in the family. (Text-fig. 18, B.)

On the other hand, although Thomas stated that the baculum of the Bornean species Rheithrosciurus macrotis is like that of Sciurus vulgaris, he tells me that he is so impressed by the improbability, on geographical and other grounds, of the two species being alike in that respect †, that he considers confirmation of the fact necessary before definite acceptance be accorded it. There is always, of course, the possibility of confusion between

the bones by taxidermists during the cleaning process.

The bacula of the S. vulgaris group are relatively well developed, but vary in size with the species, from about 14 mm.

in S. niger to 8 mm. in S. ingrami.

The foregoing account shows that the Palæarctic and American Squirrels fall into two categories by the structure of the penis and baculum :-

1. Sciurus, embracing the Palearctic species, all the Nearctic species except the one quoted below, and the Neotropical species.

2. Tamiasciurus, represented by hudsonicus and possibly related

species.

* My best thanks are due to the authorities of the Smithsonian Institution for the My best tranks are due to the authorities of the similariant institution for the generous loan of these two Squirrels. One, in winter pelage (January), was collected at Nulato in Alaska by W. H. Dall, the other, in summer pelage (September), at Tamarak Swamp, New York, by E. A. Mearns.

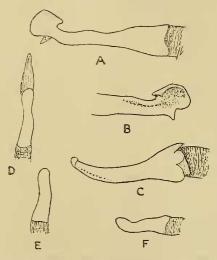
† Although Rheithrosciurus, with its grooved incisors, has always been regarded as an isolated genus, the discovery that it is really related to Sciurus (s. s.), on the

evidence of the baculum, would surprise me much less than did the discovery of the wide divergence between *Tamiasciurus* and *Sciurus* in the structure of the glans penis and the occurrence of the baculum.

2. The Oriental Species.

In Funambulus palmarum the glans is long, subcylindrical proximally, swollen and spongy in texture distally, and terminates in a longish, narrow, attenuated process, slightly or considerably inclined upwards and rising from the dorsal extremity of the swollen portion. The orifice lies at the base of this process at the right side. The baculum is a simple curved rod, concave on its upper side, convex below and tolerably gradually attenuated from the thick base to the narrow apex, which reaches to the extremity of the above-described terminal process of the glans. The

Text-figure 19.



- A. Baculum of Sciurus (Parasciurus) niger, from the left side.
- B. Apex of the same from the right side.
- C. Baculum of Protoxerus stangeri, from the left side.
- D. Baculum of Funisciurus congicus, from below, with the soft, dried, shrivelled tip of glans adherent.
- E. The same of Paraxerus cepapi, with the tip of glans removed.
- F. The same from the left side.

curvature varies apparently individually. The bone measures 10.5 mm.—that is to say, it is actually as long in this small Squirrel as in the giant *Ratufa*. (Text-figs. 18, C; 20, D.)

In Tamiodes (gen. nov.) tristriatus, regarded by Blanford as possibly nothing but a local race of palmarum, the glans is very different. It is relatively shorter and thicker, and ends in two well-marked subequal labia, one above and one below the terminal orifice. The upper labium is unmodified; but the lower, which has its inferior edge inclined upwards, is subdivided into a number of subordinate labia by deep lateral elefts, which are

represented on the lower side of the tip by grooves running obliquely backwards and inwards towards the middle line. It was clearly, I think, to a Squirrel of this genus, possibly indeed to tristriatus, that the glans penis figured and described by Tullberg as that of palmarum belonged. His figure, however, does not show such a definite lower lip as was present in the example from Malabar above described, the area beneath the upper lip being supplied with two rows of lobules representing the subdivisions

of the lower lip in my specimen. (Text-fig. 18, D.)

The difference between F. palmarum and T. tristriatus in the structure of the penis is reflected in the shape of the baculum, which in T. tristriatus, instead of being gradually curved upwards from base to apex, has the proximal three-fourths curved towards the right with the right side concave, the left convex, and the distal fourth bent up at a right angle to form a vertical branch with an expanded tip, a convex crested posterior edge and a concave anterior edge. From the inferior angle of this arises a much smaller branch directed downwards. This description is taken from a baculum, measuring 11.5 mm., taken from a specimen of tristriatus from Helwak, Satara, and preserved in the British Museum. Another baculum in that collection, taken from an unidentified specimen without locality, differs in having a less expanded apex to the upper branch, no crest on the latter and no inferior branch, the shaft being straight. It measures 11 mm., and may represent a different race or species. (Text-fig. 20, A, B, C.)

In the example from Malabar of which the glans penis was described, the apex of the upper branch projected a little way into the upper lip of the glans, and the lower branch formed the bulge at the inferior part of the base of the lower lip. The baculum, measuring 12 mm., is similar in curvature and other particulars to that of the example from Satara, except that the

inferior branch is more quadrate and not hook-like.

The two genera of Oriental Squirrels described above are a most instructive instance of close superficial resemblance associated with great differences in the glans penis and baculum. They are so much alike that Blanford was doubtful if tristriatus was more than what he would have called a "variety" of palmarum. Yet it is impossible to believe in close kinship between them; and the differences explain the occurrence of the two in the same districts in India without ever intergrading—that, at all events, I believe to be the case.

The structural characters of the two may be recapitulated as follows:—

α. Glans penis ending distally in a narrow elongated point supported by the distal portion of the baculum; the orifice on the right side near the base of the slender portion and remote from the tip of the class. Baculum a simple uncurved attenuated red

Funambulus.

Tamiodes.

The baculum of an example of Ratufa gigantea from Gokteik, N. Shan States, in the British Museum, is simple and shaped in a general way like that of Funambulus palmarum, but is relatively much shorter and stouter. It is expanded at the base, and in lateral view its upper and lower edges are respectively concave and convex, but with a sinuous outline. The distal end of the lower surface is irregularly bevelled up to the apex, which is narrowed but not pointed, and there are four subsymmetrically arranged rows of small irregularly spaced bony spicules on this distal portion, which from the dorsal or ventral aspect is seen to be slightly asymmetrical. It measures 10 mm. (Text-fig. 20, E, F.) The baculum of a specimen, referred to the same species, from

Darjiling is very similar, but more strongly bevelled and upcurved distally, the apex being a little expanded; and one of R. fellii from Yin, L. Chindwin, is also very like it. But a baculum of a captive specimen * of R. indica, without locality, also in the British Museum, is very different. It is a much larger and longer bone, about twice the length of the others if straightened, and has its distal half bent strongly upwards at an obtuse angle, a shoulder-like excrescence on each side marking the bend. This distal upturned portion is quite symmetrical, expanded basally and apically, concave laterally, hollowed inferiorly, and tridentate at the tip, the median tooth being a little longer and set further back than the laterals. This baculum, measuring in a straight line from base to apex 14 mm., may be perfectly normal. Its strongly upturned distal portion evidently corresponds to the slightly upturned denticulated, bevelled distal portion of the other bacula of the genus. (Text-fig. 20 G, H.)
Setting aside *Rheithrosciurus macrotis*, above referred to as

probably having a baculum shaped like that of Sciurus vulgaris, the rest of the Oriental genera of Sciuridæ, as Thomas showed, have bacula specialised by the development, on the upper side, of a blade which is hinged to the shaft in such a way as to be slightly movable from right to left. The blade projects backwards, and a longer or shorter portion of its posterior end is free from the shaft. Bacula of this kind belong to two main categories—one, characteristic of Callosciurus, the other of Tomeutes. But distinct as the bacula of these two kinds are in their extreme forms.

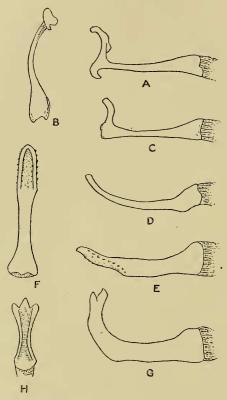
there are indications of intergradation between them †.

In Callosciurus prevosti, the type of Callosciurus, the glans is

^{*} Bacula of mammals kept in confinement are sometimes abnormal. † In his preliminary description of these bacula Thomas wrote:—"In position in † In his preiminary description of these bacula Thomas wrote:—"In position in the penis the blade points to the right, its edge cutting outwards." Again, the baculum of Callosciurus is said to have "a narrow blade set on the side of it, in the concavity of its general curvature....the greatest breadth [of the blade] is only about one-fourth to one-sixth of its length." This, however, does not agree with my observations, for I find in all the fresh or spirit-preserved material examined that the concavity of the shaft of the baculum and the blade are on the dorsal or upper side of the bone. If the blade were on the right side, the asymmetry of the baculum would be extreme and the edge of the blade would cut the right side of the vulva. I have no doubt that the function of the blade is to make a vertical cut of the integument (hymen) covering the orifice of the vagina.

long, slender, nearly straight and compressed, narrowed and pointed at the end, with the orifice just near the tip on the right side. There is comparatively little fleshy tissue enveloping the baculum, and the upper edge of the blade of the latter forms a

Text-figure 20.



- A. Baculum of Tamiodes tristriatus, from Satara, from the left side.
- B. The same from above.
- C. The same of another specimen, without locality.
- D. Baculum of Funambulus palmarum, from the left side.
- E. The same of Ratufa gigantea, from the left side.
- F. The same from below.
- G. Baculum of captive specimen of R. indica, from the left side.
- H. Distal end of the same, from the front.

hard, sharp ridge, covered merely by a coating of fine membrane, at the distal end of the dorsal side of the glans. The baculum itself is long and slender, gradually attenuated from base to point and with a sinuous curvature, being slightly concave in the

middle below and above in its distal third. The blade, about one-third of the length of the entire bone, is lodged in the distal concavity. It has a straight upper edge, not rising above the median dorsal convexity of the shaft. Its posterior third is pointed and free from the shaft. Its anterior end is attached immediately behind the slightly expanded tip of the shaft. Hence the blade is at the distal end of the shaft. The baculum above described measures 26 mm., the longest in the Sciuridæ. (Text-figs. 18,

E, F; 21, B.)

Callosciurus notatus, from Java, has the glans shorter than in C. prevosti and with a pronounced dorsal curvature in its distal half, so that its upper surface is concave, its lower surface convex. The sharp distal edge formed by the blade is more pronounced, and the orifice is situated as in C. prevosti. The baculum differs from that of C. prevosti in being relatively stouter, in having a larger thickening at the proximal end, a strongly upcurled distal half with a concave upper and a convex lower edge; but the blade, although similarly placed distally, is not so pointed and its upper edge is above the line of the edge of the shaft preceding it. (Text-figs. 18, G, H; 21, C.)

In specimens of *C. castaneoventris* from Ningpo and of *C. atrodorsalis* from Siam the shaft of the baculum resembles that of *C. notatus*, although it is less strongly curved upwards; but the blade, which is considerably longer, being nearly half the length of the shaft, is not attached to its distal end, which projects freely beyond the anterior end of the blade, the blade itself lying nearly in the middle of the dorsal concavity of the shaft. In *C. castaneoventris* the baculum measures 19 mm. (Text-fig. 21, A.)

In Thomas's preliminary account of the bacula of the Oriental Squirrels, *Ç. prevosti* was one of the species in the list of unexamined forms, whereas *C. notatus*, castaneoventris, and atrodorsalis appear in the list of species of which the baculum was examined. The remaining species of this list were caniceps,

erythræus, pluto, and sladeni.

The differences between the bacula of *C. prevosti* and *C. notatus* on the one hand and of *C. castaneoventris* and *C. atrodorsalis* on the other suggest the possibility of usefully splitting *Calliosciurus* into two genera. The characters appear to me to be at least as valuable as the presence or absence of a degenerate premolar. But it would perhaps be premature to take that course, at all events until it has been shown that the bacula of other species do not show intermediate stages in the position of the blade.

The baculum of a specimen of *Menetes berdmorei* from Kokareet (Tenasserim) in the British Museum very closely resembles that of *C. prevosti* described above, except that the shaft is straight up to the concavity containing the blade. It is convex below only at its distal end and correspondingly concave above, the blade lying in the distal concavity as in *C. prevosti* and *C. notatus*. The baculum of this species, measuring 11 mm., was held by Thomas to have a blade-somewhat connecting the types of bacula

characteristic of Callosciurus and Tomeutes. It does not seem to me that its baculum is more Tomeutes-like than that of C. notatus. The partial intergradation between the bacula of C. prevosti, the type of Callosciurus, and of T. lokroides, the type of Tomeutes, is effected, as explained below, by C. notatus and

T. vittatus. (Text-fig. 21, D.)

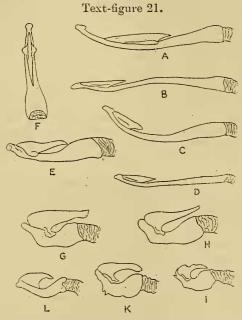
The bacula of what may be called the *Tomeutes* type differ from those of the *Callosciurus* type above described in having the shaft of the bone shorter and thicker, and the blade deeper and longer, with a shorter hinged area and a longer portion free from the shaft. The shaft is variable in length, being sometimes twice the length of the blade, the point of which falls considerably short of its proximal end or base, or sometimes a little shorter than the blade, the point of which then overlaps the base of the shaft. In all cases probably the glans penis is shorter and thicker than in *Callosciurus*.

In Tomeutes vittatus the glans penis is very like that of Callosciurus notatus, but is relatively shorter and thicker. Its upper and lower edges are parallel; along its upper runs a sharp carina formed by the edge of the blade of the baculum and ending distally in a short point. On the right side about half-way between this point and the inferior rounded angle of the distal end opens the orifice, which has a little fleshy lobe on its outer side; and from this a groove runs backwards along the right side of the glans nearly to its proximal end. (Text-fig. 18, I, K, L.)

The baculum, measuring 14 mm., although conforming in a general way to the typical Tomeutes type of baculum, is more like that of Callosciurus notatus than any I have seen. The shaft is about twice the length of the blade, very thick at the base, slender beneath the blade, with lightly convex but sinuous inferior border, and upturned at the apex, which is furnished with a small button-shaped thickening projecting an appreciable distance beyond the distal end of the blade. The latter, lying in the concavity of the upper side of the shaft, has a nearly straight, smooth upper edge, the lower edge, also nearly straight, running obliquely upwards and backwards to meet it in a point. The hinged portion ends inferiorly in an expansion on each side which, as it were, clamps the blade to the shaft, and corresponds to the lateral expansion of the blade seen in Callosciurus notatus and This species, Tomeutes vittatus, appears in castaneoventris. Thomas's list of unexamined species of Callosciurus. From the superficial resemblance between vittatus and notatus, he probably inferred that their bacula would be alike. That, however, is not the case. (Text-fig. 21, E, F.)

The baculum of a specimen of the type of the genus *Tomeutes*, namely *T. lokroides*, from Kursiong in Sikkim, preserved in the British Museum, has a much shorter shaft and bigger blade than that of *T. vittatus*, and is altogether more specialised. The shaft has a thickened proximal end with the distal third sharply upturned, making a deep, short concavity. The blade, measuring

 $8~\mathrm{mm.}$, is longer than the shaft, its blunted point overlapping the thickened proximal end of the shaft, and the upper edge of the blade rises high above the concavity of the bone. In this respect it differs from the baculum of T. vittatus, where the upper edge of the blade does not project above the concavity lying between the apex and base of the shaft. (Text-fig. 21, G.)



- A. Baculum of Callosciurus castaneoventris, from the left side.
- B. The same of C. prevosti.
- C. The same of C. notatus.
- D. The same of Menetes berdmorei.
- E. The same of Tomeutes vittatus, from the left side.
- F. The same from above.
- G. The same of T. lokroides, from the left side.
- H. The same of T. hippurus.
- I. The same of T. robinsoni.
- K. The same of T. miniatus.
- L. The same of T. tahan.

The baculum of a specimen of *T. hippurus* from Bukit Tangga, Negri Sembilan, also has the blade overlapping the proximal end of the shaft, but not to the same extent as in *T. lokroides*. The shaft, moreover, is relatively longer, with a longer concavity; the blade is not so deep and does not project so high above the concavity of the baculum as in *T. lokroides*. In a measure this

baculum serves to connect those of T. vittatus and T. lokroides.

(Text-fig. 21, H.)

The baculum of a specimen of *Tomeutes miniatus* from Bukit Kutu, Selangore, has the shaft tolerably similar to that of *T. lokroides*, but the blade is slightly shorter than the shaft and much thinner, being concavely emarginate inferiorly so that there is a larger space between its lower border and the subjacent upper edge of the shaft. There are also a few bony spikes on the inferior edge of the shaft at the base of the upturned distal portion. The bone measures 7.5 mm. This species, Mr. Thomas tells me, comes near *T. vittatus* in general characters; but the great differences in their bacula preclude the view of close kinship between the two species. (Text-fig. 21, K.)

In a specimen of *Tomeutes robinsoni*—a species akin, Mr. Thomas tells nie, to *T. lowii*—from Bukit Tangga, Negri Sembilan, the baculum has the shaft short, stout, and strongly curved, being very like that of *T. miniatus* but somewhat thicker proximally, shorter, and without trace of the bony spicules. The blade, too, is tolerably similar but shorter, with a lightly convex upper edge, with a notch and tooth. The bone measures 6 mm.

(Text-fig. 21, I.)

In a specimen of *T. tahan* (allied to *T. tenuis*), from Bukit Kutu, Selangore, the shaft is relatively longer and thinner than in the previously described species, except *T. vittatus*, and its inferior angle, very obtuse, is near the middle of the lower surface approximately beneath the point of the blade. The blade itself is short and deep, with a long hinge, a lightly convex upper edge, a strongly concave lower edge, and a narrow apex. The bone measures 5 mm. Judging from the baculum alone this species would be referred to *Dremomys*. (Text-fig. 21, L.)

The main distinctive features of the bacula of the species of

Tomeutes above described may be summarised as follows:—

a. Shaft comparatively long, about twice as long as blade, its lower edge lightly convex, its apex projecting well beyond blade; upper edge of blade not higher than line tangential to upper proximal and distal ends of shaft

ittatus

- a'. Shaft comparatively short, much less than twice as long as blade, its lower edge strongly curved or geniculate, its apex only surpassing blade slightly; upper edge of blade higher than line tangential to upper proximal and distal ends of shaft.
 - b. Angle of lower edge of slender shaft set far back almost beneath point of blade, distal portion beyond bend inclined gradually upwards; hinge nearly as long as blade tahan.

b'. Lower edge of stout shaft with pronounced angle in front of lower end of hinge, distal portion beyond angle tipped steeply upwards; hinge much shorter than blade.

c. Blade with apex not overlapping proximal end of shaft, its lower edge deeply and widely emarginate towards hinge ... miniatus, robinsoni.

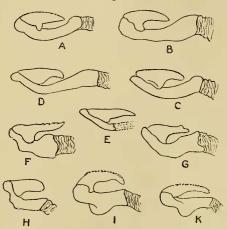
c'. Blade with apex overlapping proximal end of shaft, its lower edge nearly straight up to small concave notch by hinge.

lokroides, hippurus.

According to Thomas the following species belong to Tomeutes:—phayrei, blanfordi, pygerythrus, janetta, pryeri,

philippinensis, melanogaster, tenuis, brookei, lowii, murinus. I have not seen their bacula; but those described above are sufficient to show how variable this bone is within the limits of the genus as admitted by Thomas. The variation, indeed, is so great that it is impossible to affirm any character by which the baculum of Tomeutes can be distinguished from the bacula of Dremomys, Rhinosciurus, Tamiops, and Lariscus. It is not improbable that a careful comparison between the bacula of all the species assigned at present to Tomeutes will give useful indication of interspecific relationship.

Text-figure 22.



- A. Baculum of Dremomys lokriah, from the left side.
- B. The same of D. rufigenis.
- C. The same of D. rufigenis fuscus.
- D. The same of D. dawsoni.
- E. The same of Lariscus jalorensis.
- F. The same of Rhinosciurus robinsoni.
- G. The same of Tamiops maclellandi barbei.
- H. The same of Nannosciurus microtis.
- I. The same of N. whiteheadi.
- K. The same of N. exilis.

The baculum of a specimen of Lariscus jalorensis from Bukit Tangga, Negri Sembilan, is represented by the blade and the piece of the shaft to which it is attached. This portion of the blade is compressed and shows no angulation of its inferior border, which suggests that the upcurvature was gradual as in Tomeutes vittatus or Dremomys dawsoni. Its apex is produced as an acute angle beyond and in the same line as the upper edge of the blade, which is nearly straight, with a slightly depressed apex, and forms an acute angle with the line of the hinge very

much as in *Tomeutes vittatus*. In the latter, however, the apex of the shaft is expanded and button-shaped, not compressed as in

Lariscus jalorensis. (Text-fig. 22, E.)

The baculum of a specimen of *Rhinosciurus robinsoni* from Tiernan Island, in the British Museum, is very like that of *Tomeutes lokroides*. The shaft is short, proximally thick, distally upturned, with a short concavity, with its large blade projecting high above it and overlapping the proximal end. The upper edge of the blade is nearly straight, but is irregularly notched in its posterior half. The bone measures 10 mm. (Text-fig. 22, F.)

In a specimen of *Tamiops maclellandi barbei* from Kokareet, in the British Museum, the shaft of the baculum gradually narrows from base to apex, its distal half being upturned at an obtuse angle. The blade has a long hinge but is short, the point being very narrow, with a notch and tooth near its apex. Its upper edge is only slightly higher than a line touching the upper edge of the proximal and distal ends. The bone measures 5 mm.

(Text-fig. 22, G.)

In four species of Dremomys, namely, D. lokriah from Sikkim, D. rufigenis from H'Kauti, Chindwin, D. rufigenis fuscus from Annam, and D. dawsoni from Tatken, Chindwin, the shafts of the bacula are longish and longer than the blades. In that of D. rufigenis the proximal end of the shaft is very thick and raised, the median part is straight, and the upcurved distal end has an evenly convex edge. The upper edge of the blade is markedly convex to the apex, which falls far short of the proximal end of the shaft; its lower edge is straight with a pronounced concavity near the hinge. The baculum of D. rufigenis fuscus is sufficiently different to suggest specific distinction between the two forms. The shorter shaft is comparatively narrow proximally, its inferior edge is evenly convex, the upcurvature beginning beneath the inferior end of the hinge; the blade is larger as compared with the shaft, has a longer hinge, an evenly concave lower border, and a less convex upper border. In D. dawsoni the shaft overlaps the blade proximally to an even greater extent than in D. rufigenis, but it is not so stout, and its lower edge is inclined upwards from a point below the inferior end of the hinge as in D. rufigenis fuscus, but more abruptly, and the concavity of the lower edge does not extend up to the bottom of the hinge, the edge at this point being slightly convex. In D. lokriah the shaft is very like that of D. rufigenis fuscus, but is a little stouter distally, and the lower edge of the blade is straight ap to the point where it runs into the thickening forming the lower end of the hinge. (Text-fig. 22, A-D.)

The bacula of the species of Dremomys above described may

be contrasted as follows:-

a. Lower edge of shaft tolerably straight for the greater part of its length, distal end of shaft expanded with strongly rounded edge; blade thinner, with wide emargination close to short hinge rufigenis.

a'. Lower edge of shaft tolerably evenly convex throughout or convex beneath lower end of long hinge, distal end not expanded, without strongly convex edge.

b. Apex of blade some distance from proximal end of shaft, lower edge of blade with sigmoid curvature...... dawsoni.

b'. Apex of blade a little behind proximal end of shaft, lower edge of blade without sigmoid curvature.

c. Lower edge of blade evenly emarginate, distal end of shaft not thickened rufigenis fuscus.

c'. Lower edge of blade straight up to angular notch by hinge; distal end of shaft to which blade is hinged somewhat expanded lokriah.

In three species of Nannosciurus—N. whiteheadi from Kina Balu, N. exilis from Borneo, and N. microtis from Sarawak—the proximal end of the shaft of the baculum is not thickened and elevated, and its upper edge, as far as the hinge of the blade, is almost straight, and is parallel in a general way to the lower edge of the blade; the tip of the blade just reaches the base of the shaft. In N. whiteheadi and N. exilis the lower side of the shaft has a rounded swelling near the middle, and the distal end is only a little raised; the blade is arcuate with serrated upper edge and a narrowed point. In N. whiteheadi the apex of the shaft, to which the blade is hinged, is thicker, and the blade itself is more arcuate and more strongly serrated than in N. exilis. N. microtis the shaft has no definite inferior thickening, its distal half is bent up at an obtuse angle, the blade is not arcuate nor serrate, and the tip is bluntly rounded and scarcely narrowed in profile view. (Text-fig. 22, H-K.)

The measurements of these bacula are as follows:—N. white-

headi 5 mm., N. exilis 4 mm., N. microtis 3 mm.

In the following table the characters of the bacula of the three species of Nannosciurus, here described, are briefly summarised :-

a. Shaft with its distal half bent up at an obtuse angle without a rounded thickening near the middle of its lower surface; blade with tolerably straight, smooth upper edge and widely rounded microtis. tip

- a'. Shaft tolerably straight axially from end to end, the extreme apex a little elevated, a conspicuous thickening near the middle of the lower surface; the blade long, apically attenuated, with upper edge convex and serrulate.
 - b. Blade high and arched, with wide space between its lower edge and the shaft.....

b'. Blade lower, less arched, a much narrower space between its

whiteheadi.

edge and the shaft exilis.

The Oriental Squirrels thus fall into three main groups, judged by their bacula :-

1. Rheithrosciurus, belonging to the same group as Sciurus of the preceding section.

2. Ratufa, Funambulus, and Tamiodes, with simple bacula.

3. Callosciurus, Tomeutes, Tamiops, Lariscus, Nannosciurus, etc., which have compound bacula provided with a blade.

3. The Ethiopian Species.

In Protoxerus stangeri, as identified by Tullberg, the glans penis is elongated and nearly straight, but exhibits at the distal end of its proximal half a large swelling, showing a pair of low crests above and a pair of distally directed pointed processes below. Beyond the swelling the glans is gradually narrowed towards the apex, but the apex itself is shaped like an arrowhead, with the point slightly upturned and a pair of small

swellings just before it. (Text-fig. 23, M.) ...

The baculum of a specimen of this species from the Como River, in the British Museum, is a symmetrical bone, slightly concave above, convex towards the middle below, a little upturned at the apex, which ends in a blunt condyle-like button. On each side of the shaft in its distal third towards the apex there is a faintly defined longitudinal crest. The proximal end, or base, is much thickened, and carries a coronet consisting of five symmetrically arranged bony lobes, one being in the middle line above and two on each side, the two lower lobes being separated by a notch in the middle line below. There is no doubt, I think, that the thickened proximal end of this bone is imbedded in the tissue forming the submedian thickening of the penis described and figured by Tullberg, and, from analogy, I suspect the button-like tip of the baculum is lodged in the thickened portion of the arrow-headed apex. (Text-fig. 19, C.)

The actual length of the bone, despite the large size of the

Squirrel, is 7.5 mm.

In *Ethosciurus poensis*, as identified by Tullberg, the glans penis is quite short, and consists of a thickened proximal portion, composed of two transverse folds of soft tissue of which the posterior has a finely serrated posterior border on the upper side, and of a slender distal portion which gradually narrows from the base to the simple apex. According to Tullberg, the glans penis of this species has no baculum, but from analogy I suspect a small baculum, imbedded in the tissues, was overlooked.

In an example of Funisciurus leucostigma from Bibianaha the glans penis is not at all unlike that of E. poensis. Its proximal portion is quite short and thick, consisting of soft grooved tissue, but the distal portion, abruptly differentiated from the proximal, is a comparatively slender somewhat flexible rod, tapering apically but furnished on each side with a serrulated crest starting distally behind the tip and ending proximally on the upper side of the thickened base. These two crests define the upper from the

lateral surfaces of the process. (Text-fig. 23, E-G.)

In Funisciurus leucostigma niveatus the glans penis differs somewhat from that of F. leucostigma above described, although consisting of a short undifferentiated proximal portion, a swollen laminate and grooved median portion, and a thinner longer distal serrulated flexible portion. The median portion, however, is not so thick as in typical F. leucostigma, and the distal portion is

thicker and more irregular in shape, being markedly asymmetrical and not so sharply marked off from the swollen median portion. The orifice appears to lie in the swollen median portion beneath the proximal end of the distal portion. When at rest within the abdomen the terminal half of the distal portion lies in the prepuce and is bent like a hook, and the penis does not extend beyond the prepuce as in *Heliosciurus rufobrachium* described below. (Text-fig. 23, C, D.)

The dried distal portion of the glans of a specimen of Funisciurus pyrrhopus from Ashanti, in the British Museum, agrees in all essentials with that of F. leucostigma, except that the apex is better defined and more like an arrow-head. The baculum, a simple rod measuring about 1.5 mm., is imbedded in the serrulated area, its distal end not reaching the tip of the

glans.

In a similarly preserved part of the glans of *F. congicus*, with the tissue of the serrulated area cut away leaving the baculum exposed, the baculum is a slightly curved rod about 2 mm. in length, and the dried tissue of the apex of the glans, still attached to the distal end of the baculum, is lanceolate. (Text-fig. 19, D.)

In Paraxerus cepapi the glans is very similar to that of Funisciurus leucostigma. The proximal portion is very thick and short, and bent on itself, its convex surface having a median line of serrulations. Distally this thickened portion shows grooved flaps of soft tissue. The terminal process is very like that of Funisciurus leucostigma, being broad at the base, pointed at the apex, and provided dorso-laterally on each side with a serrulated crest. The sides of this process are, however, concave, so that the dorsal area bordered by the crests is much narrower in the middle than behind and in front. (Text-figs. 23, H, I; 19, E, F.)

The dried process of the glans of a specimen of *Paraxerus* palliatus from Zululand, in the British Museum, is tolerably similar, but the serrulated area is somewhat sharply constricted in front, so that the tip of the process is better defined and more arrow-headed in shape and the middle of the serrulated area is broad, broader indeed than its proximal end, where it rises into a crest. The baculum, measuring less than 2 mm., is imbedded in the process of the glans behind the apex and between the constrictions. (Text-fig. 23, K, L.)

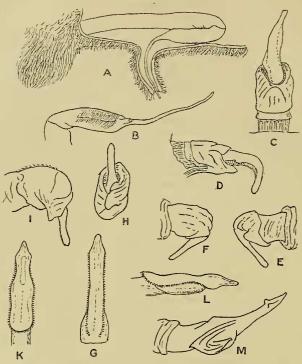
The dried condition of the distal portion of the glans penis of Funisciurus pyrrhopus and of Paraxerus palliatus makes their comparison with that of the spirit-preserved material of F. leucostigma and Paraxerus cepapi a little unsatisfactory. But the general similarity between the penes of these two so-called genera admits of no doubt. I suspect Tullberg overlooked both the baculum and the serrulated crests in the specimen he referred to

Sciurus poensis.

In an adult male of *Heliosciurus rufobrachium hardyi* the penis is of exceptional length. When extended it reaches as far as the posterior end of the sternum, and measured from its

origin just in front of the anus, it is more than half the length of the head and body. Within the abdomen its proximal portion up to the origin of the glans projects some distance beyond the prepuce. The glans is very sharply divided into two parts, a

Text-figure 23.



- A. Penis of Heliosciurus rufobrachium hardyi, retracted.
- B. Glans of the same extended, from the right side.
- C. Glans penis of Funisciurus leucostigma niveatus, from above.
- D. The same from the right side.
- E. Glans of F. leucostigma, from the left side.
- F. The same from the right side.
- G. Narrowed distal portion of the same, from above.
- H. Glans of Paraxerus cepapi, from above.
- I. The same from the right side.
- K. Narrowed distal portion of glans of Paraxerus palliatus, from above.
- L. The same from the right side.
- M. Glans of Protoxerus stangeri, from right side (after Tullberg).

proximal and a distal, nearly equal in length. The proximal portion, when at rest, is folded back beneath the distal end of the preglandular part of the penis, is dorso-ventrally expanded, and

slightly compressed and striolate laterally. Its upper portion is lightly convex, smooth, and cartilaginous, but not ossified. Its lower portion consists of softer tissue, and carries the urethral orifice on a small fleshy process at the distal extremity of its right side. The distal extremity of the glans is long, slender, flexible, and filiform, like a rat's tail. I can find no trace of baculum in it, unless the remnant of this bone is represented by a slight opacity at the distal end of the thread. (Text-fig. 23, A, B.)

In an immature male of Heliosciurus punctatus the penis resembles in a general way that of H. rufobrachium, being exceedingly long and distally slender and filiform without trace of baculum. The specimen is not well preserved, but the filiform portion appears to terminate in a small arrow-headed tip and to pass into the main body of the penis without the intervention of the swollen glandular portion carrying the orifice such as is seen in H. rufobrachium. The position of the orifice I could not determine.

The differences above described are very considerable, and if they are found to obtain in adult examples of H. punctatus, they would, I suppose, indicate a generic difference between that species and H. rufobrachium. But since the example in question is immature and poorly preserved, the examination of fresh material must be awaited ere a decision on the point is reached.

Temporarily setting aside the penis of the example of Heliosciurus punctatus above described, the characters of this organ as shown in the other genera may be tabulated as follows:—

a. Penis exceedingly long, the distal portion of the glaus forming a long, flexible thread-like termination without baculum Heliosciurus.

a' Penis quite short; the distal portion of the glans shorter, stouter, rod-like, not filiform, and provided with a baculum.

b. The narrow rod-like distal portion flexible, with a finely serrulated crest on each side, and carrying a minute baculum near

b' The narrowed distal portion not flexible, without serrulated crests, but supported throughout by a relatively large baculum. Protoxerus.

It must be remembered, however, that the characters assigned to the penis of *Protoxerus* and *Æthosciurus* are taken from Tullberg's descriptions and not from my own observations.

Despite the differences between the penes of these genera, there are certain significant features they have in common. The glans is divisible into two parts, a swollen proximal portion carrying the urethral orifice and a more slender terminal portion.

The most primitive type appears to be that of *Protoxerus*, where the terminal portion is relatively stout, moderately long, less sharply distinguished from the swollen proximal portion, without serrulated crests, and supported by a well-developed baculum, the proximal thickened end of which is probably lodged in the thickening of the glans, while the apex extends to the arrow-headed tip of the thinner distal portion.

In the next stage, exemplified by Æthosciurus, Paraxerus, and Proc. Zool. Soc.—1923, No. XVI.

Funisciurus, the baculum is reduced to a small rod imbedded near the apex of the distal portion, which is consequently flexible. This portion, however, is specialised by the development of a finely serrulated crest on each side, and is more sharply marked off from the swollen portion of the glans, upon which it is capable of being moved up and down.

Finally in *Heliosciurus*, the highest type, the distal portion is developed into a flexible filiform process without baculum, the thickened portion of the glans is longer and simpler, and the

preglandular portion of the penis is greatly lengthened.

Returning to Protoxerus, it may be recalled that Thomas drew attention to the likeness between its baculum and the baculum of Ratufa. Unfortunately the penis of Ratufa is unknown; but a similarity may be traced between the glans of Protoxerus and of Funambulus if, as I suppose, the orifice opens in Protoxerus on the swollen part of the glans at the base of the terminal slender portion. The chief differences in that case between them will be reduction in the size of the baculum in Protoxerus and specialisation of the glandular thickening from which the slender terminal portion arises. In any case the likeness between the bacula and penes of Protoxerus and Funambulus is greater than the likeness between those same organs in Funambulus and Tamiodes.

4. The African Ground-Squirrels.

In the African Bristly Ground-Squirrels the glans penis is relatively large, turns downwards at the apex, and has a well-

developed terminal baculum.

In Eucerus erythropus the glans is long, and consists of two parts, a subcylindrical proximal piece composed of soft, striate or otherwise sculptured tissue, and a terminal smooth, compressed piece with an elevated, convex upper edge which curves downwards distally to end in a rounded apex, behind which the inferior border is concave. The upper edge ends posteriorly in a twist near the middle of the upper side of the glans. At the distal end of the spongy portion beneath and a little to the right of the middle line just behind the base of the compressed portion, the orifice opens. (Text-fig. 25, E-H.)

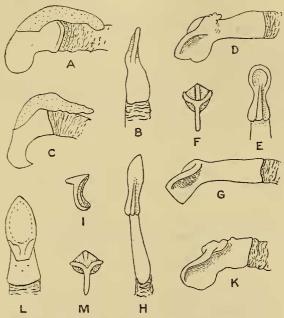
The baculum, measuring 8-9 mm., conforms to the shape of the distal portion of the glans, and consists of a stout, short cylindrical proximal piece and a compressed blade, sometimes rounded, sometimes hooked backwards at its inferior apex. The upper side of the bone is slightly concave; but carries a cartilaginous crest, sometimes partially ossified, which runs backwards some distance behind the proximal end of the bone and represents the distal dorsal crest of the glans. (Text-fig. 24, A-C.)

The glans of Geosciurus capensis is tolerably similar, with a similar dorsal crest ending in a twist proximally, but the distal portion is not compressed, but gradually narrows to end in a

slightly expanded truncated apex. The orifice is in the median ventral line, nearer the tip of the glans than in *Euxerus* erythropus. (Text-fig. 25, A-D.)

The baculum, measuring 8 mm., has a much longer proximal subcylindical portion than that of *Euxerus*, and the upper

Text-figure 24.

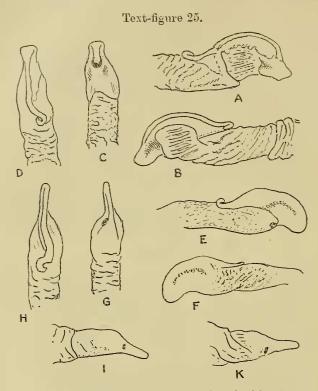


- A. Baculum of Euxerus erythropus, from the left side.
- B. The same from above, without the cartilaginous crest.
- C. Baculum of another specimen, ticketed E. erythropus.
- D. Baculum of Geosciurus capensis, from the left side.
- E. Apex of the same from above.
- F. Apex of the same from the front.
- G. Baculum of Atlantoxerus getulus, from the left side.
- H. The same from above.
- I. Tip of the same from the front.
- K. Baculum of Xerus rutilus, from the left side.
- L. The same from above.
- M. Tip of the same from the front.

surface of the terminal portion is an elongated area rather more than twice as long as broad, with a low median crest, a rounded spatulate hollowed apex, and distinctly constricted sides. The lower side of the terminal portion is developed into a median vertical crest. (Text-fig. 24, D-F.)

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The baculum in Atlantoxerus getulus, measuring 7 mm., has a still longer proximal portion, or "handle," than in Geosciurus, and the blade is simpler. Its dorsal area is apically asymmetrical and not markedly spatulate, and the sides are scarcely constricted,



- A. Glans penis of Geosciurus capensis, from the right side.
- B. The same from the left side.
- C. The same from below.
- D. The same from above.
- E. The same of Euxerus erythropus, from the right side.
- F. The same from the left side.
- G. The same from below.
- H. The same from above.
- I. The same of Cynomys ludovicianus, from the right side.
- K. The same of Marmota marmota.

but the median crest seen in *Geosciurus* is present. The inferior crest of the blade is also asymmetrical, curving towards the left inferiorly. (Text-fig. 24, G-I.)

In Xerus rutilus the "handle" of the baculum is shorter than

in Geosciurus and no longer than in Euxerus; but the upper surface of the blade is very wide, much wider than the "handle" and shaped like a spearhead, with convexly rounded sides and a sharp point, the width being rather more than half the length; its dorsal median crest is much less pronounced than in Geosciurus and its apex is not spatulate and hollowed. The inferior crest is similar to that of Geosciurus. The bone itself measures 6 mm.

(Text-fig. 24, K-M.)

Of the above-described bacula that of Atlantoxerus comes nearest to the baculum of typical Sciuridæ in the length of the proximal cylindrical portion or handle; Geosciurus comes next, and Xerus and Euxerus last with the proximal portion quite short. In the gradual differentiation or specialisation of the blade the series runs Euxerus, Atlantoxerus, Geosciurus, Xerus; but which of the four is the most primitive type I am quite unable to say. It is interesting, however, to note that the most widely separated types are found in Yerus and Euxerus, which until recently were referred to a single genus, although Geosciurus and Atlantoxerus had been severed from Xerus.

a. Distal portion of baculum a compressed blade not expanded above, its upper edge narrow..... Euxerus. a'. Blade of distal portion of baculum laterally expanded more or less above, its upper surface spatulate or subspatulate with a longer or shorter median crest behind. b. The upper surface forming an elongated oval plate with uniformly convex sides, pointed at the apex and with a short crest behind; proximal portion of baculum only about half the length of the distal

b'. The upper surface much narrower, with sinuous sides and a longer crest; proximal portion almost as long as the distal or longer.

c. Sides of the upper surface strongly constricted, the terminal area apically rounded and hollowed

Geosciurus.

A point of systematic interest connected with the glans penis and baculum of the Xerinæ is the complete absence of resemblance between them and the corresponding organs in the African Squirrels, Protoxerus, Funisciurus, and Paraxerus, which were associated with Xerus by Forsyth Major on the evidence derived from skulls and teeth.

5. The Sousliks and Marmots.

The glans penis of Citellus I have had no opportunity of examining, but the bacula of several species are preserved in the collection of the British Museum. In all cases the bone consists of an elongated shaft, broad at its proximal end and narrowing distally to the apex, which is upturned and expanded into a wide, sometimes double disc with denticulated margin.

The simplest type is the baculum of a specimen of C. mongolicus from Chifu. The shaft is abruptly expanded at the base, nearly straight when viewed from above or below, but with the upper margin concave, the lower convex. The slightly raised distal expansion, hollowed above like a shovel, is irregularly semicircular in shape, and has a continuous unevenly denticulated edge, without median notch; and the apex of the shaft of the baculum projects forwards as a process from its lower surface. The bone measures about 3 mm., and the width of the distal expansion is about half the length of the shaft. (Text-fig. 26, A, B.)

The baculum of a specimen of C. leursi from Jalisco, in Mexico, has the shaft very broad at the base, whence it gradually narrows to the expansion. Its upper and lower edges are nearly straight from the lateral view, but from the dorsal view the shaft is seen to bend distally slightly towards the right. The disc is relatively and actually much wider than in C. mongolicus, and its right side is produced more than the left; but its edge is continuous, without median notch and more regularly denticulated than in C. mongolicus. There is, moreover, no process representing the tip of the shaft on the under side of the disc. The bone measures 5 mm., and the width of the disc is almost equal to the length of the shaft. (Text-fig. 26, C, D.)

In two examples of C. mexicanus, one from the City of Mexico, the shaft differs from that of C. mongolicus and leursi in having its upper edge abruptly inclined downwards and distally towards the disc; and the disc itself differs in having a deep median notch in its margin and in being much more strongly bent upwards, so that its hollow is much deeper and more triangular in shape. As in C. mongolicus, the apex of the shaft is continued as a short process projecting from the lower surface of the disc in front a little beneath the notch. The bone measures about 5.5 mm, and the greatest width of the disc across its posterior angles is less than half the length of the shaft. (Text-fig. 26, E, F.)

In a specimen of C. 13-lineatus from Minnesota the shaft is intermediate in shape between that of C. mexicanus and of C. leursi; but the disc differs from that of the other species in having its edge broad and furnished with two rows of teeth. It is, moreover, very definitely divided into a right and left lamina by a wide and moderately deep median notch in front, and it is somewhat abruptly upturned. The tip of the shaft shows as a low, indistinctly defined rounded boss on the under side of the disc just below the notch. The bone measures 5 mm, and the width of the disc is about half the length of the shaft. (Textfig. 26, G-I.)

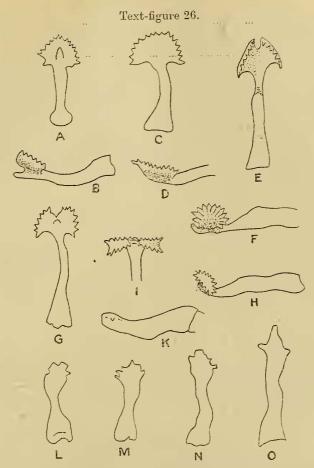
a. Edge of the apically widely notched disc broad and armed with two

a'. Edge of the disc narrow and armed with a single row of teeth.

b. Disc nearly vertically upturned, with a narrow median notch in front: upper surface of shaft distally geniculate.....

mexicanus.

b' Disc a little upturned, without median notch; shaft not distally geniculate above.



- A. Baculum of Citellus mongolicus, from below.
- B. The same from the left side.
- C. Baculum of C. leursi, from below.
- D. Apex of the same from the left side.
- E. Baculum of C. mexicanus, from above.
- F. The same from the left side.
- G. Baculum of C. 13-lineatus, from below.
- H. The same from the left side.
- I. Apex of the same from above.
- K. Baculum of Cynomys ludovicianus, from the left side.
- L. The same from above.
- M. The same of another specimen, from below.
- N. Baculum of Marmota marmota, from below.
- O. The same of another specimen.

c. Disc comparatively small, its width about half the length of the shaft, the tip of the shaft projecting as a process be-..... mongolicus.

c'. Disc very wide, its width almost equal to the length of the shaft, the apex of which forms no projection beneath it in

In Cynomys ludovicianus the glans penis is short, its proximal two-thirds being stout and subcylindrical and its distal third forming a quite narrow terminal process sharply defined from the thicker portion. The orifice lies on the right side close to the base of the narrowed end. The baculum, measuring 4 mm. in length, lies in the narrowest portion and reaches its apex. It is broader at the base and tip than in the middle and is slightly asymmetrical. Its upper edge is very slightly concave, its lower edge mesially geniculate, the apex being irregularly

denticulated. (Text-figs. 25, I; 26, K-M.)

In Marmota marmota the glans penis is shaped very much like that of Cynomys, but is relatively a little shorter. The orifice opens similarly on the right side at the base of the narrowed terminal process and the baculum, measuring only 7 mm., and lying in the narrowed piece is a slightly asymmetrical bone with expanded base and expanded irregularly denticulate apex. It is not quite alike in two specimens examined, and I am unable to affirm any character apart from size by which it may be distinguished from the baculum of Cynomys. (Text-figs. 25, K; 26, N, O.)

It may be recalled that Tullberg many years ago described the glans penis of Marmota [Arctomys] as very small and asymmetrical, with the opening on the right side behind the tip, which carries a small baculum. The male genitalia of Cynomys he described as like those of Marmota; but, what is more interesting still, he declared the male genitalia of Tamias to be also very

similar to those of Marmota.

6. The Subfamilies of Sciuridae.

For the following grouping of the genera of non-volant Squirrels, constituting the Sciuridæ, I take the glans penis and the baculum as supplying characters of primary value. It may be objected that these characters apply only to one sex; but I do not think it can be doubted that corresponding differences occur in the females and merely await discovery. The baculum has been examined either by Mr. Thomas or myself in all the principal genera, and the penis by Tullberg and myself in a considerable number of them. As subsidiary characters I have used the ears and feet, leaving alone cranial and dental characters, the study of which by Thomas, Forsyth Major, and many American authors has led to no very satisfactory result apart from the steady but unavoidable and convenient multiplication of genera and subgenera.

Subfamily Sciurinæ.

Glans penis apically expanded, compressed and upturned, enveloped behind the upturned tip in soft swollen tissue. Baculum large, with compressed terminal blade hollowed on the right side, which carries inferiorly a short downwardly directed process.

Ears relatively long, more tubular at the base, with large

angular antitagral flap.

Feet with fourth digit the longest; the plantar, carpal, and metatarsal pads normal and relatively simple.

Genera: Sciurus, with subgenus Tenes* for persicus; all the American subgenera or genera, Neosciurus, Parasciurus, Echinosciurus, etc., except Tamiasciurus; ? Rheithrosciurus.

Distribution. Holarctic and Neotropical Regions and ? Borneo (Rheithrosciurus),

I feel compelled to include *Rheithrosciurus* provisionally in this group, pending confirmation or refutation of Thomas's statement that the baculum is like that of *Sciurus*. In other external characters supplied by the ears and feet it is certainly unlike other Oriental species and comes nearer to *Sciurus*. On the evidence at present available I should judge it to be a highly specialised member of the Sciurinæ as above defined.

Subfamily Tamiasciurinæ.

Distinguishable from the Sciurine, which it resembles in cranial and other external characters, by the structure of the penis, which is relatively long and slender and tolerably evenly attenuated from base to apex, and flexible throughout owing to the suppression of the baculum.

Genus Tamiasciurus.

Distribution. Nearctic Subregion.

The general resemblance between *Tamiasciurus* and the typical Sciurinæ suggests that it is a specialised offshoot of that group. It is a very remarkable fact that the extreme differentiation of the penis does not appear to be correlated with other variations from the Sciurine type.

In the structure of the penis *Tamiasciurus* shows to a certain extent a convergent resemblance to the African genus *Helio*-

sciurus (see below, p. 238).

Subfamily Funambulinæ.

A highly diversified group of genera, with the glans penis exceedingly variable in size and structure and the baculum either

^{*} Thomas, Ann. & Mag. N. Hist. (8) iii. p. 468 (1909).

relatively very large (Funambulus, Tamiodes), relatively small (Ratufa, Protoxerus), minute (Funisciurus, Paraxerus, Ethosciurus), or absent (Heliosciurus). It is, however, when present, always a simple bone without the spatulate expansion at the apex seen in the Sciurine, without the accessory blade of the Tomeutine, and without the compressed downturned lamina of the Xerinæ. The ears are always relatively shorter and wider and less tubular at the base than in the Sciurine, but are without the peculiarities of the ears of the Xerinæ and altogether better developed.

Genera: Funambulus, Tamiodes, Ratufa, Protoxerus, Æthosciurus, Funisciurus, Paraxerus, Heliosciurus, and probably the other African genera admitted by Thomas. including possibly even Myosciurus.

Distribution. Oriental and Ethiopian Regions.

When the genera are better known, this group will perhaps be split up into several subfamilies. So far as my observations go, the genera fall into the following sections by the characters established in this and my previous paper :-

a. Tamiodes, with a thick glans penis with terminal labiate orifice and a large baculum with its distal extremity bent

upwards at a right angle to the rest of the shaft.

3. Funambulus, with the glans terminally narrowed, the simple orifice on its right side, some distance behind the tip of the glans, and the baculum large and gently curved upwards distally.

y. Ratufa, with the baculum relatively quite small, curved as in Funambulus, but stouter and bevelled below distally; (glans unknown); the feet in their pad development quite different

from those of the other genera.

d. Protoxerus, with the glans possessing a median swollen area carrying the orifice, and an elongated narrower distal portion supported by a relatively small baculum not differing greatly from that of Ratufa, but with a button-like apex and a scalloped proximal end.

e. Funisciurus, Paraxerus, Ethosciurus. Glans with a marked median grooved or laminate swelling and a slender distal portion as in Protoxerus; but the distal portion flexible, laterally serrulate, and carrying a minute undifferentiated

baculum close to the apex.

4. Heliosciurus. Penis and glans exceedingly long, the glans with narrower, longer swelling, and exceedingly thin, long filiform distal portion without trace of baculum.

Of other genera that have been established, Tamiscus, recently dismembered from Paraverus, probably falls into section ϵ . But whether Epixerus comes into d or e I am unable to surmise. Probably an examination of the glans penis and baculum will

settle the doubtful question as to the affinities of the genus with *Protoxerus* or *Funisciurus*. Of the genitalia of *Myosciurus*, I know nothing beyond Thomas's statement that the baculum is simple as in other African genera. The position of *Myrsilus* is also doubtful.

Subfamily Callosciurine.

Glans penis variable in shape and length according to the baculum; the orifice close to the tip on the right side. Baculum long and slender or short and stout, slightly or strongly upturned distally, and always provided with an accessory blade, movably jointed to the concavity of the upper surface.

Ears as in Funambuline.

Feet, where known, intermediate in structure between those of the more primitive types of the Funambuline (Funambulus) and the specialised genus Ratufu.

Genera: Callosciurus, Menetes, Tomeutes, Rhinosciurus, Lariscus, Dremomys, Tamiops, Nannosciurus, and probably others.

Distribution. Oriental Region from India to China and Borneo.

This group may perhaps be regarded as a specialised offshoot from the Funambulinæ. The simplest type of baculum, e.g. that of *Callosciurus*, may be derived from that of *Funambulus* by the addition of the blade. But the subterminal position of the orifice is as in the Sciurinæ.

Subfamily XERINÆ.

Glans penis, where known, with a strongly convex crested upper distal edge and a downwardly directed, rounded or truncated apex. Baculum with a stout, longer or shorter subcylindrical proximal portion, and a compressed downturned terminal blade with a median crest above and frequently a laterally expanded upper surface.

Ears more or less reduced, but with large fleshy antitragal

thickening.

Feet with strong fossorial claws and the third digit the longest. Fur scanty and harsh. An additional tuft of superciliary vibrissæ over the posterior corner of the eye.

Genera: Atlantoxerus, Xerus, Euxerus, Geosciurus. Distribution. Africa from Morocco to Cape Colony.

The structure of the penis and baculum alone serves to negative the idea that this group of African Ground-Squirrels is closely akin to certain African arboreal Squirrels, an idea which prompted the proposal by Major of such names as *Protoverus* and *Paraxurus* for two genera of the latter category. The Xerinæ, indeed, are in addition distinguishable from the rest of the

African genera of the family by their ears, feet, fur, and the additional tuft of superciliary vibrisse, and by the cranial characters pointed out by Thomas in his paper on African Squirrels.

Subfamily MARMOTINÆ.

Glans penis, at least in Marmota and Cynomys, very small, a diminutive copy indeed of that of Funambulus but with the point not upturned by the curvature of the baculum; also somewhat resembling that of Funisciurus and Paraxerus, except that the proximal thickening and the terminal narrowed piece are structurally simple and less sharply differentiated. Baculum also relatively very small, highly specialised with a symmetrical terminal, denticulated lamina in Citellus, but ending simply with a few irregularly placed denticles in Marmota and Cynomys.

Ears simplified, without tragal or antitragal thickenings, but with a hairy expansion of the anterior rim extending into the

cavity beneath the supratragus.

Feet with fossorial claws and the third digit not shorter than the fourth.

Genera: Marmota, Marmotops, Cynomys, Citellus with many subgenera, ? Tamias, and Eutamias.

Distribution. Holarctic Region.

Although admitted as a subfamily in many text-books, this group was not granted that rank by some competent judges, e. g. Forsyth Major and Miller, on account of the closeness of its kinship with the true Squirrels. It appears, however, to be sufficiently well characterised to be admitted.

I have provisionally included *Tamias* and *Eutamias* mainly on the strength of Tullberg's statement that the genitalia are similar to those of *Marmota*, but also because *Tamias* and *Citellus* are alike in the presence of large cheek-pouches, a character in

which they differ from all the typical Squirrels.

Nevertheless the feet of the only example of this group I have seen in a fresh state, namely a female of Eutamias quadrivittatus, are not like those of Citellus, and hardly differ from those of the Squirrels. The ears, too, do not show the special features characteristic of those of Citellus, Marmota, and Cynomys, but are more like those of Sciurus. More extended observations on the two genera are required to determine their exact systematic status. Possibly they will prove to be worth ranking as a special subfamily—Tamiine.

7. The Flying Squirrels.

The Petauristidæ were classified by Thomas in 1908*. Setting aside *Petaurista*, he took the genus *Sciuropterus*, already shown by Heude and Forsyth Major to be composed of heterogeneous

elements, and pointed out that it is divisible by the structure of the teeth into six genera:—Sciuropterus, type russicus, for the Palearctic species; Trogopterus for xanthipes from China; Belomys, type pearsoni, Pteromyscus, type pulverulentus, Petaurillus, type hosei, and Iomys, type horsfieldi, from various parts of the Oriental Region, each containing one or more species besides the type. Furthermore, he divided Sciuropterus into four subgenera: Sciuropterus itself; Glaucomys for the North American rolans and the Himalayan fimbriatus*; Hylopetes, containing many species ranging from Nepal to the Malay Islands, with everettii as the type; and Petinomys, ranging from Ceylon into South India and the Malay Islands, with lugens as type.

Owing to lack of material, I can contribute very little to what has been already established as to the affinities of the genera of this family. The outstanding result of my examination of the bacula is the complete severance of *Eoglaucomys* from *Glaucomys*. This suggests that further surprises may be in store for him who

has the time and opportunity to carry on the work.

The penis and baculum are as variable in the Petauristidæ as in the Sciuridæ. The penis itself is only known to me in two genera, Eoglaucomys and Hylopetes, of which one specimen of

each, preserved in alcohol, has been available.

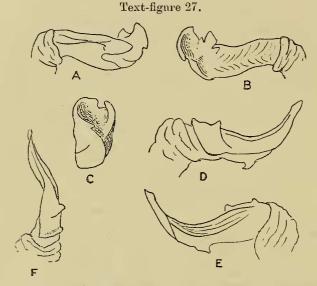
In Eoglaucomys fimbriatus the glans is stout and tolerably long, a little stouter just beyond the middle than at the base, and slightly upcurled but not appreciably narrowed at the end. On the left side above, just before the tip, there are three processes in a line, the first and third short and semiconical, the second or middle one much higher and roughly three-sided. Beyond these the apex of the glans forms a lamina hollowed on the left side, and beneath this there is a rounded area with a fleshy flap defined by a groove which passes backwards on to the right side, where the area in question is narrowed and runs backwards, being defined above and below by a groove. The orifice appears to be situated towards the posterior end of the upper groove, and from the orifice two more grooves run backwards to the proximal end of the glans. (Text-fig. 27, A-C.)

The baculum, measuring 7.5 mm., is exceedingly short and occupies only the distal half or less of the glans. It is furnished with several processes, and agrees tolerably closely in shape to the shape of the end of the glans. It is indeed the bony processes of the baculum, enveloped in soft tissue, which give shape to the end of the glans; but the rounded area of the glans below the distal hollow is wholly composed of soft tissue, no portion of the baculum entering it. The proximal end of the baculum forms a short, stout rod, shorter than the terminal toothed portion and emarginate below. Considering the former association,

^{*} This species was subsequently separated from ${\it Glaucomys}$ as the type of the subgenus ${\it Eoglaucomys}.$

suggested by their names, of *Eoglaucomys* with the North American *Glaucomys*, the differences between their bacula are very striking and suggest that the resemblances between the genera, which induced Thomas in his revision of the Petauristidæ to refer *fimbriatus* to *Glaucomys*, are purely convergent. The differences between their bacula are apparently indeed greater than the differences between the bacula of any other two species. (Text-fig. 29, H–K.)

In Hylopetes althougher the glans penis is very different from that of Eoglaucomys. The distal half of the glans is narrowed and curved considerably towards the left and upwards at an



A, B. Glans penis of *Eoglaucomys fimbriatus*, from right and left sides.
 C. Apex of the same from the front.

D, E, F. Glans penis of *Hylopetes alboniger* from right side, left side, and above.

angle of about 135°. On the left side of the upturned portion there is a crest running downwards from the apex and ending near the middle of the lower convex surface in a well-marked compressed point. Near the base of the glans on the upper surface there are two crests, one in front of the other and defining a kind of saddle-shaped area; these crests pass downwards on to the right side of the glans. I could not find the orifice of the organ of the specimen examined. (Text-fig. 27, D-F.)

The baculum, measuring 13 mm., is shaped distally like the distal portion of the glans, having the same upward and sinistral curva-

ture. There is a well-developed crest on its left side, passing from the apex down to the inferior tooth which is the termination of the crest. But although the baculum is long and extends throughout the length of the glans, it shows no trace of crests or processes behind the termination of the crest inferiorly. This baculum differs from that of *Eoglaucomys* in its length, its simple apex, and the lateral inferior crest. (Text-fig. 28, C, D.)

Of this baculum I have seen two specimens, one taken from the spirit-preserved example from the Himalayas in the Zoological Society's collection, the other from an example from Mishmi in

the British Museum.

The baculum of a specimen of *Hylopetes phayrei* from Burma, in the British Museum, measures 11 mm., and agrees very closely with that of *H. alboniger*, but is less markedly upcurled distally

and is provided with a larger crest. (Text-fig. 28, E.)

Hylopetes, it may be recalled, was regarded by Thomas as a subgenus of Sciuropterus. Since the baculum of Sc. russicus does not appear to have been described, it is impossible to give an opinion as to the precise status of Hylopetes. But if, as appears to me probable, the baculum of Sciuropterus russicus resembles that of Glaucomys volans, full generic value should, I think, be

given to Hylopetes.

The baculum of an example of Petinomys fuscocapillus from Cevlon, in the British Museum, is a tolerably stout bone with a sinistral curvature like that of Hylopetes, the right side being convex, the left side concave, but it has no very marked upward curvature, the upper edge being slightly sinuous and the apex a little raised, almost as in Hylopetes phayrei. The apex, however, is broader than in Hylopetes and somewhat spatulate, the left margin of the shallow apical hollow being raised into an angular tooth behind. On the lower side of the bone there is a strong crest divided by a notch, about in the middle of the bone, into a short proximal and a long distal portion. The latter, which is angled behind, forms a sinuous curve towards the left, but does not ascend on to the left-hand side of the bone distally, as in Hylopetes, but terminates on the lower side of the expanded spatulate apex. The baculum measures 11 mm. (Text-fig. 28, F-H.)

In view of the affiliation by Thomas of *Petinomys* with *Hylopetes* as subgenera of *Sciuropterus*, it is interesting to note the broad general resemblance, associated with marked differences, between their bacula.

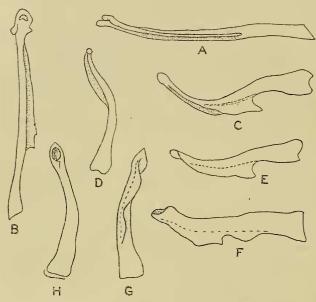
The baculum of *Glaucomys volans*, judging from two specimens in the British Museum, one of which is ticketed Virginia, is exceedingly long and slender, slightly sinuous in its proximal third, and inclined slightly upwards distally. The extreme apex is bifid, the lower process being rounded, the upper more pointed. On the left side there is a long crest running from the summit of the upper terminal process and ending abruptly behind the left side about one-third of the distance from the proximal end of

the bone. It lies over a well-marked groove, and there is a second shallower groove on the right side of the bone. The bone

measures 12.5 mm. (Text-fig. 28, A, B.)

Despite its straightness and apical notch, this baculum is similar in type to that of *Hylopetes*, the crests on the left-hand side of the two corresponding closely. The crest in *Glaucomys* terminates on the left side of the bone instead of passing on to its lower surface as in *Hylopetes*. The surprising differences

Text-figure 28.



- A. Baculum of Glaucomys volans, from the left side.
- B. The same from below.
- C. Baculum of Hylopetes alboniger, from the left side.
- D. The same from below.
- E. Baculum of H. phayrei, from the left side.
- F. Baculum of Petinomys fuscocapillus, from the left side.
- G. The same from below.
- H. The same from above.

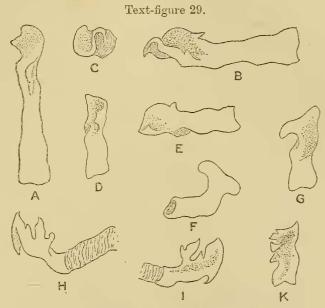
between the bacula of Glaucomys and Eoglaucomys have already

been mentioned under the description of the latter genus.

The baculum of a specimen of *Belomys* (?) trichotis from Yin, Chindwin, in the British Museum, is hardly longer than that of *Eoglaucomys*, but is otherwise very different from it. The proximal portion consists of a stout subcylindrical "handle," sharply geniculated where it passes into the abruptly upturned distal portion, which ends in a wide lamina, shaped like a

hammer-head and lying obliquely and transversely, the shorter right-hand branch projecting farther forwards than the longer left-hand branch. This baculum is quite unlike that of any other species of the Petauristide examined. (Text-fig. 29, F, G.)

The baculum of an example of *Petaurista philippensis* from Kanara, in the British Museum, is a long, stout bone, gradually



- A. Baculum of Petaurista philippensis, from above.
- B. The same from the left side.
- C. Apex of the same from the front.
- D. Baculum of Petaurista sp.? from above.
- E. The same from the left side.
- F. Baculum of Belomys trichotis, obliquely from behind.
- G. The same from above.
- H. Baculum of Eoglaucomys fimbriatus, from the left side.
- I. The same from the right side.
- K. The same from above.

narrowing from the base to the slightly expanded and upturned distal end, which, when viewed from the front, is seen to be shaped rather like the widened spout of a jug, the lower rim of the spout being evenly rounded. From the side this terminal lamina has a rounded upper border, a rather deeply emarginate and thickened distal border, and a nearly straight, obliquely ascending, thickened posterior border ending inferiorly in a small

tooth. Just below the hollow on the left side there is a small crest ending above in another small tooth. The bone measures

20 mm. in length. (Text-fig. 29, A-C.)

The baculum of another but unidentified and unlocalised species of *Petaurista* in the British Museum differs in some well-marked characters from that of *P. philippensis*. It measures only 8 mm. owing to the shortness of the proximal portion, which does not exceed the distal portion in length. The latter has its hollowed surface looking more to the left, the upper or right-hand rim being more, and the lower or left-hand rim less elevated than in *P. philippensis*, and its distal rim is not curved over and spout-like. If the ossification of the baculum proceeds backwards from the distal to the proximal end, it is possible that the difference in the length of this bone in *P. philippensis* and the unidentified species is a matter of age. (Text-fig. 29, D, E).

The following table shows how the genera examined may be

distinguished by their bacula:-

. Baculum with crest running from the comparatively small and simple apex backwards along the left or under side of the bone.	
b. Baculum nearly straight, comparatively long and slender; apex bilobed, crest confined to left side	Glaucomys.
b'. Baculum shorter, stouter, more curved; apex undivided, crest wholly or partially ventral.	
c. A single crest curving distally up on to the left side of the bone to the apex, which is simple, not spatulate	Hylopetes.
c'. A supplementary crest behind the main crest, which is entirely ventral; apex spatulate	Petinomys.
 Baculum without lateral or ventral crest, with expanded com- plex apex. 	
d. Distal end of baculum abruptly upturned and ending in a two-headed or hammer-shaped lamina	Belomys.
d'. Distal end of baculum not abruptly upturned, the apex expanded, more or less hollowed, and complicated with accessory processes.	
e. Apex of baculum hollowed, irregularly spatulate, with small accessory processes	Petaurista.

on the left side Eoglaucomys.

e'. Apex of baculum armed with uprising spiniform processes